THE ECOLOGY OF STRANGLER FIG SEEDLING ESTABLISHMENT

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ABSTRACT. Hemiepiphytic or "strangler" fig seeds are dispersed by vertebrates to establishment sites on potential host trees. Despite the importance of figs in rain forests and considerable interest in their ecology, little has been known about their early life history because it occurs in the canopy. In this paper I review work related to fig seed germination and seedling establishment and summarize my recent field experiments in the Bornean rain forest canopy to provide a synopsis of current information on fig seedling ecology. The emerging picture suggests that fig seeds germinate readily anywhere if they get enough moisture. For subsequent survival and growth, water, nutrients, and light are required, but the most limiting factor in the canopy is water stress, even in perhumid rain forests. Given a good establishment site such as a large knothole or other place on a host tree where water is trapped and nutrients accumulate, fig seedlings can take advantage of high light levels and grow rapidly. However, such sites are rare and figs also face insect seed predation and herbivory as important mortality factors in the canopy.

INTRODUCTION

Ficus is a species rich pantropical genus containing all known growth forms of woody plants: epiphytes, lianas, hemiepiphytes and free-standing trees. Besides the domestic fig, *Ficus carica,* it is that quintessential tropical plant, the strangler fig, for which the genus is best known. More than half of the 900 species of *Ficus* in the world are hemiepiphytes, commonly referred to as stranglers (Corner 1958, Janzen 1979, Putz & Holbrook 1986). Hemiepiphytic figs germinate in the canopies of host trees from seeds dispersed by vertebrates, and spend the first part of their lives as epiphytes until their extending roots reach the ground. At this point, the growth behavior varies from species to species. Some completely engulf and kill their host tree, taking over its place in the forest, while others maintain a relatively modest root to the ground and depend on their host for support throughout life (Putz & Holbrook 1986). Whether they become free standing trees or not, hemiepiphytic fig species are all commonly referred to as stranglers, due to the ability of their roots to anastomose as they wrap around the host tree.

Figs are recognized as a major component of tropical forest ecosystems (Janzen 1979, Leighton & Leighton 1983, Whitmore 1985, Terborgh 1986). This is not due to their individual abundance, which is often not great (e.g. Todzia 1986), but the fact that their fruiting phenology and quantities of fruit they produce make them particularly important for frugivorous vertebrates. Figs have population wide asynchrony in fruiting as a byproduct of their pollination system. Their production of fruit year-round has now been widely documented (Janzen 1979, Milton *et al.* 1982, Windsor *et al.* 1989, Milton 1991, Kjell-

berg & Maurice 1989, Lambert & Marshall 1991). This makes them a reliable resource for vertebrates, and in many tropical forests, figs appear to be one of the most important resources utilized by animals during otherwise fruit-poor periods (Leighton & Leighton 1983, Terborgh 1983, 1986, Wrangham *et al.* 1993). This has led to their being called "keystone species" (sensu Gilbert 1980) because of their critical role in sustaining vertebrate populations, and also their indirect benefit to other infrequently fruiting plant species which are dependent on the presence of frugivores for seed dispersal (Leighton & Leighton 1983, Terborgh 1986). The importance of gaining a better understanding of the ecology of hemiepiphytic figs and their role in the rain forest community has been widely espoused (Janzen 1979, Putz & Holbrook 1986, McKey 1989, Soule & Kohm 1989, Howe 1993)

The unusual life history traits of hemiepiphytic figs and their evolution have also been a focus of considerable interest (Dobzhansky & Murca-Pires 1954, Corner 1976, Ramirez 1977, Whitmore 1985, Putz & Holbrook 1986, Daniels & Lawton 1991, 1993). Certain aspects of fig biology have been relatively well studied, such as the mutualistic pollination system involving Agaonid wasps (Janzen 1979, Wiebes 1979, Bronstein & McKey 1989). However, hemiepiphytic fig seedling establishment occurs in the canopy, and the difficulty of access has hampered progress in understanding many aspects of fig ecology surrounding seed dispersal, seed germination and seedling establishment.

The factors that limit figs to colonizing only a small proportion of available host trees in the forest have remained a puzzle since Corner (1940) first pointed out the problem, saying "Considering how vigorous they are and how easily their

seeds are distributed, it is a problem why strangling figs do not occur on most big trees in the forest." Galil & Meiri (1981) have speculated that limitations to seed germination and seedling establishment could be critical, and my recent research has been aimed at addressing some of the gaps in our knowledge about the early stages of fig life history (Laman 1994, a, b, in press).

In this paper, I summarize the results of my recent research on strangler fig ecology in Borneo, placing them within the context of previous studies to provide a synopsis of our current understanding of how strangler figs get established on their hosts.

Fig Seed Germination

Once fig seeds are dispersed to potential establishment sites, what factors affect whether they will germinate and grow successfully? A combination of laboratory experiments and more recent field studies are beginning to elucidate the critical conditions.

Bessey (1908) showed that light was required for the germination of *F. aurea* in Florida. Galil & Meiri (1981), working on *F. religiosa,* confirmed that seeds would not germinate in total darkness, but showed that low light levels were adequate to trigger germination. Fig seeds appear to germinate readily at light levels inadequate to support growth, such as deep understory shade in my experiments on *F. stupenda* (Laman 1994) and also *F. dubia* and *F. xylophylla* in lowland Borneo. This suggests that the response to light is not for the purpose of waiting until the conditions get brighter, as is often the case with gap specialists in the seed bank. The importance of soil bacteria for fig seed germination reported by Ramirez (1976) has not been apparent in subsequent studies. Galil & Meiri (1981) used sterile conditions and sterilized seeds, and obtained good germination of *F. religiosa,* while Titus *et al.* (1990) obtained successful germination of *F. pertusa* and *F. tuerckheimii* on sterile petri plates. If bacteria are helpful, they are apparently not a limiting factor, at least not for all fig species. Well washed fig seeds on filter paper readily germinate if kept moist, indicating that contact with soil is not required to trigger germination (Galil & Meiri 1981, Titus *et al.* 1990, Midya & Brahmachary 1991).

Several lines of evidence point to the primary importance of moisture for fig seed germination. The presence of a viscous seed coating with water absorbing properties has been found to be widespread among fig species (King 1888, Bessey 1908, Ramirez 1976, Michaloud & Michaloud-Pelletier 1987). This coating may aid the seed in retaining and absorbing enough moisture to ger-

minate. Dry conditions can prevent germination. For example, Titus *et al.* (1990), and Galil & Meiri (1981) both reported that fig seeds that were regularly dried out by the sun never germinated. Titus *et al.* (1990) found that even with daily watering, seeds on the ground did not germinate in a sunny location where the ground dried regularly, and Galil & Meiri (1981) showed that continuous wetting with a sprinkler generated high germination on ground where no germination occurred without watering.

To explore further the factors affecting germination under natural conditions, I conducted experiments on the hemiepiphyte *F. stupenda* in Gunung Palung National Park, West Kalimantan, Indonesian Borneo. An initial experiment comparing germination between well lit locations in gaps and poorly lit locations in the understory gave results supporting the observations of Titus *et al.* (1990) and Galil & Meiri (1981) mentioned above (Laman 1994). The experiment was a balanced factorial design which examined the effect of three different substrate types (soil, moss, bark) under each light treatment. ANOVA showed that both light environment and substrate type had significant effects on the germination success of *F. stupenda* seeds (light: $F = 7.42$, $p = 0.03$; substrate: $F = 8.59$, $p = 0.02$). The interaction term between light and substrate was not significant ($F = 1.14$, $p = 0.38$). Germination level was higher in the poorly lit understory sites for all three substrate types, averaging 68% overall compared with 48% overall germination in well lit sites. Seeds in poorly lit sites may have had better germination because they remained more consistently moist. Seeds planted in the high light gap locations were exposed to several hours of sun per day and observed to become desiccated. Germination was best on soil, intermediate on moss, and lowest on bark substrates. The water retaining capacities of the different substrates could be a possible explanation for the differences in germination success among substrates.

Germination in natural sites in the canopy was examined in a large scale experiment in which 20 *F. stupenda* seeds were planted in each of 336 canopy sites spread among 45 dipterocarp trees (Laman in press a). Substrate type was the only site variable that had significant effects on germination in the canopy. The water holding capacities of canopy substrate types have been measured by ter Steege and Cornelissen (1989), who divided them into four categories. In order of decreasing water retention, these were: bryophyte mats, dead wood, humus/litter, and bark. In my experiment, substrates with good moisture retention, such as rotting wood, soil, or moss yielded good germination rates, ranging from 30

to 42%. Among these, rotting wood substrate, such as is often found in knotholes and on broken branches was the best. Leaf litter and bark substrates, which appeared more prone to desiccation, had lower germination levels of 16 and 8%. Other variables such as light level, soil quantity, and height above ground had no significant effects on germination. These experiments under natural conditions thus support the idea that moisture is the primary factor required for successful germination, and this makes sense in terms of the hemiepiphytic lifestyle of these plants.

Although not an effect on the process of germination itself, seed predation may be an important factor reducing fig establishment at the seed stage. In my canopy experiments, I found an arboreal species of ant in the genus *Pheidole* that harvested fig seeds. This ant was present in 24% of 45 dipterocarps surveyed, and had a highly significant negative effect on the numbers of seeds germinating in canopy planting experiments (Laman in press a). Interactions with seed harvesting ants could be complex, however, and involve secondary dispersal as well as seed predation (Laman in press b, Kaufmann *et al.* 1991).

One question often raised with regard to plants dispersed by vertebrates is whether passage through a gut enhances or is required to trigger germination. Fig seeds pass through the guts of most fig consumers intact, with the exception of certain seed predators such as pigeons in the genus *Treron* in Asia (Lambert 1988). I have found that fig seeds germinate readily from various bird, primate, and civit feces. Most of the experiments described above used seeds that did not pass through vertebrate guts, but seeds nonetheless germinated readily (e.g. 94% of control seeds, Laman in press a). If there is an acceleration of germination by passing through a vertebrate (e.g. Midya & Brahmachary 1991) this may be most likely due to water absorption that can begin while in the animal gut. Passing through a vertebrate gut is certainly not essential for germination per se, although in reality survival through guts is required since it it the only way for hemiepiphytic fig seeds to get dispersed to suitable establishment sites in the canopy. Unlike terrestrially establishing plants which can frequently recruit offspring directly below the parent, suitable recruitment sites on new host trees are unlikely to be available below the parent for a hemiepiphyte. Successful dispersal is thus imperative for hemiepiphytes.

Fig Seedling Establishment

Following germination, what factors are essential for successful seedling establishment and survival during the epiphytic stage of life? By combining the observations of earlier descriptive studies with more recent experimentation, a picture is beginning to emerge.

The sites in host trees at which hemiepiphytic figs become established are generally described as having an accumulation of organic matter or soil in a crotch or knothole where the seedling has access to abundant water and light (Bessey 1908, Richards 1952, Ramirez 1977, Putz & Holbrook 1986). Access to the rotten core of the host tree may also be beneficial (Galil 1984, Putz & Holbrook 1986). In a survey of fig seedling distributions in a Zimbabwe savanna, Guy (1977) found most figs in rough barked trees. In another study in a savanna environment, Putz & Holbrook (1989) studied the rooting habits of figs in palm trees in the llanos of Venezuela. At this site nearly half of the Copernicia palms supported a hemiepiphytic fig. The palm's marcescent leaf bases trapped large quantities of organic matter and provided excellent establishment sites, demonstrating the densities that hemiepiphytic figs can attain given a high availability of suitable establishment sites. Daniels & Lawton (1991, 1993) studied *F. crassiuscula*, unusual strangling fig in the subgenus *Pharmacosycea* in the cloud forest of Monteverde, Costa Rica. This species has a unique viny sapling stage in its life history distinguishing it from the more typical hemiepiphytes of the subgenus *Urostigma*. It showed preferences as an adult for colonizing certain host species but the distribution of younger plants did not indicate clear patterns of germination site preferences.

The establishment positions of figs have been examined in two surveys carried out in rain forests, both of which were limited to fig individuals with roots to the ground. These studies can thus provide a picture of the kinds of sites where growth of hemiepiphytic figs is successful. Michaloud & Michaloud-Pelletier (1987) studied figs in Gabon where they found that trees with better light exposure within their crowns tended to be colonized by figs. Figs were also more likely to occur in trees with other epiphytes. Of 94 hemiepiphytic figs, they found that 81% had established at sites of damage or decomposition in tree crowns such as knotholes, crotches, or broken branches. Figs established in undamaged locations were mostly in the crotches of large branches. In a survey of figs in Kutai National Park, East Kalimantan, M. Leighton (unpublished data), found hemiepiphytic figs of mid to upper canopy layers to most often occupy large, long-lived trees in the family Dipterocarpaceae or the ironwood tree *Eusideroxylon*. Comparing establishment position categorized as trunk, crotch, or limb sites, Leighton showed that figs on dipterocarps were established in crotches 76%

of the time, while on *Eusideroxylon*, 75% of figs had established along the large horizontal limbs characteristic of this species. While these studies give a general picture of where figs have successfully established, without information on the relative abundances of different establishment site types, these patterns cannot be clearly distinguished from random establishment, as pointed out by Daniels & Lawton (1991). In addition, more specific information about the site characteristics where the seedling originally established are obscured by the growth of the plant by the time roots reach the ground.

In order to directly examine the characteristics of establishment sites that promote *F. stupenda* seedling survivorship and growth, I monitored the canopy planting experiment described above over the course of one year (Laman, in press a). Establishment success was low especially considering that the best available sites in each of the 45 trees were selected for seed planting. Only 85 (1.3%) of the 6,720 seeds planted were surviving as seedlings at the end of one year, and only three seedlings showed steady and vigorous growth throughout the year. Knotholes were by far the best establishment locations, having ten fold greater seedling survivorship than crotches, branch surfaces, and sites on tree boles. The reason that knotholes are superior establishment sites became apparent in the analysis of the effects of site variables on seedling success. Substrate type had a highly significant effect on seedling survivorship, just as it had on germination, and rotting wood and moss were the best substrates for fig seedlings. Knotholes contained these good substrate types more frequently than the other site types. Water stress and herbivory were the principal observed causes of seedling mortality.

In parallel with the experimental plantings in natural canopy sites, I also grew *F. stupenda* seedlings in planter boxes raised into the canopy to compare the relative quality of canopy sites to the resources available in a planter of known volume (Laman in press a). My planters contained two liters of soil and were attached against upper tree boles in such a way that stem flow as well as rain would enter the planters. Survivorship and growth of fig seedlings in these planters were far greater than in natural canopy sites. All the seedlings alive in planters at the end of the year were of similar size or larger than the largest seedlings planted in natural sites. For seedlings in the planters, which all had similar access to soil and water, growth was strongly correlated with light level. In natural sites, locations with the highest light levels actually had poorer seedling growth, probably due to more severe water stress. Nutrients are unlikely to be as important a limiting factor for fig seedlings as water. Putz & Holbrook (1989) found no evidence that *F.*

pertusa or *F. trigonata* seedlings were nutrient limited, and studies of epiphyte communities have shown them not to be nutrient limited (Nadkarni 1981, 1984). Thus water availability appears to be the primary attribute of an establishment site important for fig seedlings. If they have access to enough water, fig seedlings can take advantage of high light and grow rapidly. Knotholes and other sites such as crotches with large amounts of organic deposits are therefore probably good sites largely due to their ability to trap and hold water.

The importance of water for hemiepiphytic *Ficus* seedling establishment is also supported by other lines of evidence. The physiological ecology and anatomy of these plants show characteristics for dealing with water stress, such as thick cuticles, sunken stomata, and a multiple epidermis (Putz & Holbrook 1986). Humidity and moisture availability are well known to be primary factors in determining the distributions of epiphytes, both on a scale of heights within tree crowns, and across forest types (Sugden & Robbins 1979, Benzing 1983, ter Steege & Cornelissen 1989, Luttge 1989). Thus it is not surprising that this is also a critical factor for figs during the epiphytic stage of their life.

DISCUSSION

Since moisture level seems critical to trigger germination, seeds that are dispersed during a dry period might be unlikely to encounter moist enough conditions to germinate. This raises the question of how long fig seeds might be able to last in a state of dormancy due to lack of water. This could be of considerable importance, especially in more seasonal climates, where figs fruiting during the dry season might produce no offspring unless the seeds could remain viable for several months. Since figs fruit throughout the year even in seasonal forests (Kjellberg & Maurice 1989, Windsor *et al.* 1989, Bronstein *et al.* 1990, Milton 1991), it would be of interest to know the fate of seed crops produced during dry seasons. I found that seeds stored for up to several months under field conditions showed decreased but still substantial germination, but no germination after a year. Galil & Meiri (1981) report that seeds of *F. religiosa* stored up to three years in a laboratory showed good germination. This suggests the possibility that there could be a canopy fig seed bank, at least during dry seasons.

One intriguing observation about hemiepiphytic fig seedlings has been that they are rarely observed growing on conspecific fig trees, despite the presence of potential establishment sites and presumed high seed input levels (Laman pers. obs., Titus *et al.* 1990). Titus *et al.* tested the

hypothesis that fig trees were secreting autotoxic substances which prevented successful colonization in a set of experiments in Monteverde, Costa Rica. Their results provided no evidence for toxicity on fig trees, however, and they suggested the possibility of pathogens preventing establishment on fig trees, or perhaps that fig seedlings could be fusing with conspecific host trees. In my seed planting experiments with *F. stupenda,* one treatment was to plant seeds in the crowns of *F. stupenda* adults (Laman in press a). Such locations did not adversely affect germination, however, so there was no support for the possibility of autotoxicity from my study either.

Putz & Holbrook (1986) have reported the occurrence of intraspecific root fusion in several species of *Ficus,* raising the possibility that seedlings establishing on adult figs could fuse to their hosts. More recently, Thomson *et al.* (1991) reported that some selected *Ficus* individuals were genetic mosaics with different genotypes present on different branches. Although Thomson *et al.* reported high levels of genetic mosaics among the trees they selected, it is unknown how widespread this phenomenon is in natural *Ficus* populations. Although fusion may occur in some cases, the low incidence of figs on other figs could be accounted for simply by limitations to seedling establishment. Mortality factors, such as seed predation and herbivory, are likely to be higher near the mother plant, and could result in very low probabilities of seedlings surviving on the mother tree.

For rain forest hemiepiphytic figs, sites with optimal conditions for establishment appear to be very scarce. If successful seed dispersal to good sites alone was the major factor limiting fig recruitment, then I would have expected much higher establishment success in my canopy seed planting experiment than was observed. Therefore, the relatively low abundances of adult figs in rain forests compared with the number of potential host trees could be primarily due to limitations to seedling establishment, as Galil & Meiri (1981) have speculated.

What little is known about the demography of hemiepiphytic figs suggests a population structure very different from that of the typical forest tree. Leighton (unpublished data), whose survey included figs of all sizes with roots to the ground, found a low ratio of juveniles to adults, suggesting that once they got a root into the ground, juveniles had a high probability of reaching adulthood and did so quickly. Daniels & Lawton (1991, 1993) studying *F. crassiuscula* in Costa Rica, conducted a complete inventory of all individuals in one area, and also reported low numbers of juveniles compared with adults. My observations in the canopy also indicate that juveniles with and without roots to the ground are both relatively rare. These observations suggest that mortality of figs once their roots reach the ground may be relatively low. Thus, the critical stages for the regulation of fig populations are likely to be during the epiphytic phase.

The species richness of the genus *Ficus* has long been recognized, particularly the within-habitat diversity that is seen in many tropical forests (Corner 1940, Janzen 1979, Hammel 1986, Todzia 1986, Michaloud & Michaloud-Pelletier 1987). Janzen (1979) provided a number of reasons that could help account for the coexistence of multiple fig species, including having no pollinators in common, successful pollination at low population densities, asynchronous fruiting, having seeds dispersed by many vertebrates, and having many vegetative life forms. However, he does not consider how multiple species with very similar life forms could coexist. For example in my study area in Borneo, over twenty species of hemiepiphytic figs are present. While some of these differ in their preferences for certain habitats or levels in the canopy (Laman 1994), the general pattern is one of broad overlap. It thus remains an intriguing question how the diversity of these hemiepiphytic species is maintained.

It has been observed that epiphytes in general are abundant, but that with the exception of some very moist habitats like cloud forests, the epiphytic biotope is seldom filled (Bennet 1986). Benzing (1981) has proposed a hypothesis to explain the coexistence of multiple epiphyte species on identical hosts and substrates. His proposal is derived from 'lottery for living space' models (Dayton 1971, 1975, Sale 1977), and suggests that an inability to saturate potential establishment sites with seeds, combined with patchy and shifting target sites, could account for multiple species with identical requirements to coexist. This idea was further extended to plants in general by Grubb (1986). My work with *F. stupenda* has provided the first experimental evidence for the factors which limit fig establishment in the wild, and it seems highly likely that other fig species face similar limitations. If *Ficus* species are unable to colonize all good sites, either due to dispersal or establishment limitations or both, individuals of different species may not compete with one another for space. This situation could allow many species to coexist while exploiting very similar lifestyles as hemiepiphytes in the rain forest canopy.

CONCLUSIONS

In this paper, I have generalized from studies done on a broad variety of fig species to draw out what appear to be the key elements of the

ecology of hemiepiphytic fig seedling establishment. The following main points have emerged:

1) To germinate, fig seeds need continued high humidity. Substrates with good moisture retention promote germination in the canopy.
2) For young fig seedlings to survive and grow, they need water, nutrients and light, but water seems to be the most limiting in the canopy. Sites such as knotholes which have good water retention are thus superior establishment sites.
3) As with many terrestrial plants, seed predation and herbivory also appear to be important sources of mortality for hemiepiphytic fig seedlings.
4) Limitations to establishment in the early stages of fig life history could have interesting implications for the maintenance of fig species diversity.

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